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BOTANICAL GAZETTE

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ARE ROOTS AEROTROPIC?[1]

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(WITH FIVE FIGURES)

I. HISTORICAL REVIEW.

AFTER noting the peculiar curvings and contortions that roots of *Zea Mays* exhibited when growing in water, especially when their tips were just touching the surface of the water or were slightly immersed, Molisch[2] formulated the hypothesis that these roots were affected by a poverty of oxygen in their immediate vicinity, and through their curvings were brought into a richer supply of that gas. In pursuance of that thought, he sought to determine whether roots of other seedlings would not also show definite responses to the influence of various gases. In determining this point, Molisch employed only one form of apparatus, which is here described.

The chamber containing the gas to be used was a wide-necked bottle, closed with a plate of hard rubber in which were cut one or two slits 2^{cm} high by 1.5 to 2^{mm} wide. A strip of cork was fastened to the neck of the bottle in such a position that the seedlings, when pinned to it, were supported in front of and very close to the slits. The bottle was laid, with the slits in a vertical position, on a glazed dish, and was covered with a large bell jar lined with moist filter paper. Light was excluded.

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[1] LXVIII Contribution from the Botanical Laboratory of the University of Michigan.

[2] MOLISCH: Ueber die Ablenkung der Wurzeln von ihrer normalen Wachsthumsrichtung durch Gase (Aerotropismus). Sitzungsber. Akad. Wiss. Wien 90: 111. 1885.

The roots of *Pisum sativum* and *Zea Mays* were subjected to the application of various gases diffusing or streaming in mass from the slits, and the reactions of the roots were termed aerotropic. Only those responses to the application of oxygen, hydrogen, carbon dioxid, and nitrogen are considered in my paper, as the other gases used by Molisch were poisonous, and might produce chemotropic or traumatropic reactions.

The striking similarity in the results of Molisch's experiments —namely, that regardless of the species of seedling or the gas used, whether it were a stream of pure oxygen, of oxygen of a lower pressure than the normal, of nitrogen, or of carbon dioxid, the majority of the roots in every case made an initial curve toward the source of the gas and later turned away—looks suspicious. His own explanation of these phenomena is that the curves both toward and away from the gas chamber were due to the presence of an optimum pressure of the gas for longitudinal growth. If this were true, it would seem to make the response simply a mechanical one.

Several features of Molisch's work are subject to criticism. To thrust needles through the cotyledons, as he did, is objectionable for several reasons. To take seedlings directly from the sawdust and support them before the slits is objectionable, since injurious substances often occurring in sawdust effect curvatures in roots, which do not show until some time after the seedlings have been set up. The gases which streamed out of the slits were not moist, except in the experiments with CO_2 and possibly pure oxygen. This condition would tend to bring about hydrotropic curves. Too few seedlings were used to establish certain conclusions. The data of the experiments lack details as to growth of seedlings, degree of curvature, and other minor points. Lastly, the position of the root at the conclusion of the experiment is accepted for record, regardless of the numerous curves, positive and negative, which this root made during the continuance of the experiment. Since the paper by Molisch nothing on this subject has appeared.

The present investigation of the supposed aerotropism of roots was conducted in the Botanical Laboratory of the University of Michigan during the years 1900–1902, under the supervision of Professor Frederick C. Newcombe, to whose valuable suggestions and constant assistance is largely due whatever of merit this paper may possess. It is with pleasure that I here acknowledge my indebtedness to him.

II. EXPERIMENTAL INVESTIGATION.

It has been my purpose to determine the following points as definitely as possible: whether roots are aerotropic under natural conditions; and whether they are aerotropic under any conditions. Observations have been made of the effect of oxygen, hydrogen, carbon dioxid, and, as a test, illuminating gas, these being allowed to flow against one side of roots in gaseous form or dissolved in gelatin blocks. This is the same as the effect of a less and a greater pressure of oxygen than the normal atmospheric pressure.

1. With roots in water.

In the series of experiments under this head, the seedlings were grown in filtered tap-water and placed parallel to one chamber, or between two chambers of gas, which usually had a parchment membrane closure.

At the outset several methods of experimentation were employed to determine whether roots of *Zea Mays* grow straight in water if supplied with a larger proportion of oxygen than usual. In one series, seedlings having roots from 10 to 15^{cm} in length were secured to the sides of inverted air chambers, without membranes, immersed in the water, the kernels of corn being above water, and the root tips just below the lower edge of the chamber. The root tips were thus from 5 to 10^{mm} from the air in the immersed chamber, but 9^{cm} or more from the air above the water in the larger chamber. Observations showed that of 20 seedlings used, 7 turned toward the air in the immersed chamber, 4 away, 3 in other directions, and 6 remained straight.

In another series, seedlings supported, as in all the following experiments when necessary, between two strips of moist blotting paper held firmly to small pine rods by rubber bands between the seedlings, were suspended over a chamber which was connected with a gasometer of oxygen, and had a finely perforated membrane closing the upper end through which the oxygen was allowed to bubble slowly up toward the roots. The root tips were kept not more than 5 mm from the membrane. Of 87 seedlings thus supported, only 14 grew even approximately straight.

In a third method, seedlings were supported in a Novy jar containing filtered water saturated with oxygen under an atmosphere of pure oxygen. After the water had been saturated, the cover was slightly lifted to avoid confining the stems in an atmosphere of pure oxygen. Every four hours the seedlings were transferred to another Novy jar of water saturated with the same gas. A control experiment was prepared with the same number of seedlings in ordinary filtered tap-water. There was no apparent difference in the behavior of the roots in two preparations. Of 25 seedlings used in the first preparation, 7 only were growing straight at the close of the thirteenth hour.

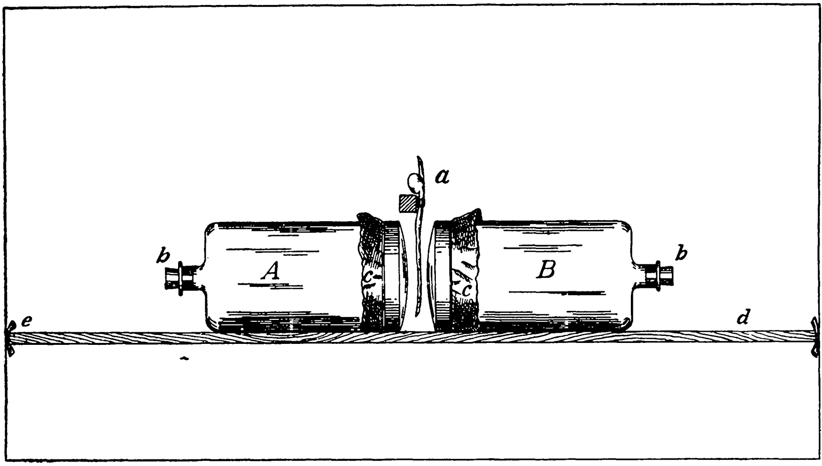

FIG. 1.—*A*, chamber containing air; *B*, chamber containing CO_2; *a*, seedling supported on wooden bar; *b*, rubber stopper; *c*, parchment membrane; *d*, strip of pine; *e*, small piece of rubber tubing.

Evidently, from these experiments no proofs have been found to justify Molisch's hypothesis that roots of *Zea Mays* in their curving in water are turning from a position in which the water is poor in oxygen to a position in which it is richer in that gas.

We must seek farther for the cause of the curving of these roots when growing in a water medium.

Other seedlings were grown in water, and placed parallel to membranes of immersed gas chambers, as shown in *fig. 1*. In the first series of experiments only one gas chamber was used, and this contained air. An explanation of the following table, in which are recorded the results, will suffice for most of the other tables found in this paper. The plus sign (+) indicates a curvature toward the supply of oxygen, and the minus sign (−) a curvature away. Only those roots which turned and continued thereafter growing toward the air chamber are counted as positive. The reverse of this rule is used in determining the negative curves. Under the zero sign (0) are classified all other curves and roots growing straight. It is noted that of 362 seedlings, including those of corn, radish, popcorn, and pumpkin, nearly as many turned away from the supply of oxygen, or the air chamber, as toward it, and more than half (206) were neutral. The angles of curvature were slight.

TABLE I.

(Plus sign indicates curve toward higher proportion of oxygen.)

Species	No. of individuals	Period: hours	Temperature of water	+	−	0	Angle
Zea Mays (field corn)	86	22–24	22–29°	24	12	50	10–45°
Raphanus sativus...	104	24–96	....	33	15	56	10–45°
Zea Mays (popcorn)	120	20–24	20–30°	18	36	66	5–90°
Cucurbita Pepo	52	20–24	16–29°	9	9	34	5–60°
Totals	362			84	72	206	

In the second series of experiments the pressure of carbon dioxid was increased above the normal on one side of the root by saturating the water frequently with that gas or by passing a slow stream of CO_2 continuously through the water, other conditions being the same as in the preceding experiment. It might be expected that the roots would turn from the CO_2 toward the supply of oxygen in the air chamber. The following table seems to indicate faintly such a response, where 39 radish seedlings were positive, as opposed to 24 that were negative or indefinite.

TABLE II.

(Plus sign indicates curve toward higher proportion of oxygen.)

Species	No. of individuals	Period: hours	Temperature of water	Initial length of root in cm.	Saturation with carbon dioxid	+	—	o
Raphanus sativus	10	48–120	20°	3–4	Once	6	1	3
Raphanus sativus	19	72	20°	3–4	Several times	11	7	1
Raphanus sativus	34	14–20	20°	3–4	Continuous stream	22	5	7
Totals	63					39	13	11

These seemingly aerotropic curvatures are invalidated, however, by those of another experiment, tabulated below, in which 166 seedlings of *Cucurbita Pepo*, *Raphanus sativus*, and *Zea Mays*, placed parallel to gas chambers containing CO_2, and a mixture of CO_2 and air (as in *fig. 1*), gave only 37 curves away from the source of CO_2 as opposed to 129 that were either turned toward that gas or were neutral. That the majority of the curves in the two experiments were in opposite directions relative to the position of similar gases indicates that the curves were not aerotropic.

TABLE III.

(Plus sign indicates curve away from gas chamber.)

Species	No. of individuals	Period: hours	Temperature of water	Initial length of root in cm.	In chambers		+	—	o	Angle
					% CO_2	% air				
Cucurbita Pepo ..	29	24–48	25°	2·7	100	..	4	2	23	5–45°
Raphanus sativus.	40	20–30	....	1–6	100	..	5	6	29	5–45°
Zea Mays........	44	9–22	24–31°	1–6	100	..	9	8	27	5–45°
Zea Mays	45	18–23	21–25°	1–7	75	25	17	6	22	5–60°
Zea Mays	8	5.5	25°	2–5	50	50	2	..	6	5–45°
Totals........	166						37	22	107	

In a series of experiments following these, similarly prepared, with the root tips not more than 2 to 5^{mm} from each membrane, the results could not be interpreted as showing aerotropism, since of 135 seedlings of lupine and radish, 46 turned toward the supply of oxygen, 39 away, and 50 were neither positive nor negative.

Finally, to increase the difference in the oxygen pressure on opposite sides of the roots as much as possible, the water in which the roots were supported opposite a chamber of air was prevented, by the device illustrated in *fig. 2*, from replenishing its supply of oxygen which was exhausted through respiration. A small aquarium was chosen which was hermetically sealed by weighting down a glass cover (*F*) on a cushion of rubber (*E*) cemented securely to the upper edges of the aquarium. The chamber (*B*) containing air was a rectanglar glass dish, 14^{cm} by 8^{cm} by 4^{cm}, supported, at angles between 20 and 45° to the horizontal, by pressing in small pieces of rubber tubing (*a*) between the ends of the dish and the sides of the aquarium. No membrane was used to inclose the gas. When the required seedlings (*C*), which had been growing in a vertical position in a damp chamber from 12 to 24 hours, were supported before the air chamber so that their tips extended 1 to 3^{mm} below the upper edge of the chamber and 1 to 5^{mm} away from it, the aquarium, already partly filled, was now completely filled with water, the cover pressed down, and the water above the roots replaced through tube *L* by gas

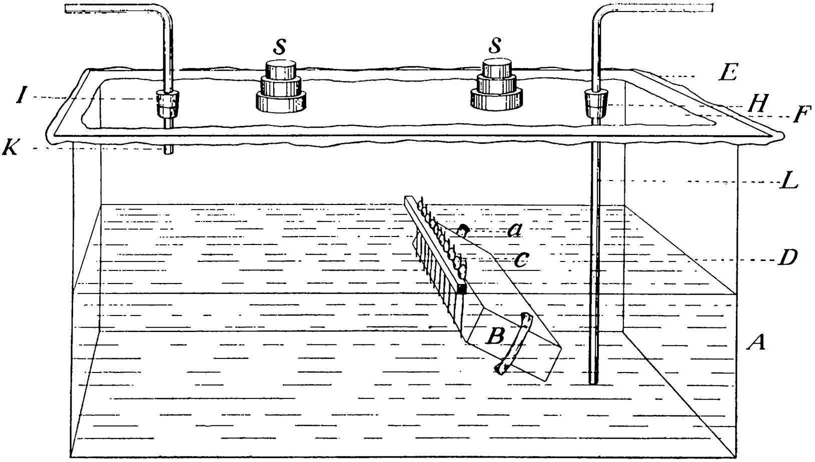

FIG. 2.—*A*, aquarium; *B*, chamber containing gas; *C*, seedlings; *D*, height of water; *E*, rubber cushion; *F*, glass cover; *H*, aperture in cover; *I*, rubber stopper; *K*, glass tube through which gas enters; *L*, glass tube for escape of water; *S*, weights; *a*, rubber tubing.

brought in through tube *K*. In such a contrivance the oxygen pressure in the water, which was reduced through respiration, would be continually renewed on the side facing the air chamber.

Table IV shows no aerotropic curves with the 54 seedlings of *Cucurbita Pepo*, 40 of which were neutral, while the remaining 14 were divided equally between positive and negative. The angles of curvature were not large and the growth was slight at first, due to insufficient pressure of oxygen. However, as more and more oxygen diffused from the chamber the roots grew more rapidly.

TABLE IV.

(Plus sign indicates curve toward air chamber.)

Species	No. of individuals	Period: hours	Temperature of water	Initial length of root in cm.	Gas above water		+	—	o	Angle	Growth
					% CO_2	% air					
Cucurbita Pepo.	16	10	27°	3-9	10	90	2	4	10	5-45°	Little first 6 hrs.
Cucurbita Pepo.	18	10	28	3-9	30	70	3	2	13	5-45°	Little first 6 hrs.
Cucurbita Pepo.	20	22	27	1-3	60	40	2	1	17	5-20°	Little first 4 hrs.
Totals......	54						7	7	40		

When the water above the gas chambers was replaced by mixtures of hydrogen and air in varying percentages, approximately the same results were obtained both in curvature and growth, as shown in Table V.

TABLE V.

(Plus sign indicates curve toward air chamber.)

Species	No. of individuals	Period: hours	Temperature of water	Initial length of root in cm.	Gas above water		+	—	o	Angle	Growth
					% H	% air					
Zea Mays (popcorn) ..	18	7	25°	3-9	10	90	..	2	16	5-30°	Good growth
Cucurbita Pepo	18	12	30	2-4	25	75	2	1	15	5-90°	Considerably retard'd
Cucurbita Pepo	18	10	25	2-4	33⅓	66⅔	..	4	14	5-20°	Slight during first 6 or 7 hrs.
Zea Mays (popcorn) ..	19	21	25	3-5	50	50	3	2	14	10-60°	Not apparently retarded
Zea Mays (popcorn) ..	16	22	..	...	75	25	4	2	10	......	Slight during first 5 hrs.
Totals......	89						9	11	69		

The duration of the experiments was necessarily short, since the roots could not be readjusted to the air chamber without altering the conditions. It is noticeable that of the 143 seedlings thus tested, 16 turned toward the air chamber, 18 away, and 109 were not responsive. The angles were generally very slight.

In the foregoing series of experiments, in which the roots were immersed in water with the oxygen pressure so reduced as to retard growth beyond the usual retardation in water, the presence of air within a few millimeters of the root tips induced no aerotropic curves.

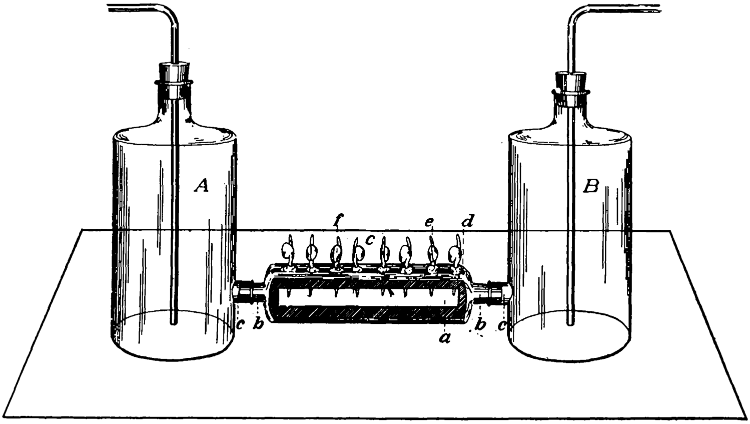

FIG. 3.—*A*, chamber filled with various gases; *B*, chamber containing air; *C*, chamber connecting *A* and *B;* *a*, glass side-wall of chamber *C;* *b*, cork sealed in end of chamber *C;* *c*, opening into bottle; *d*, position of groove; *e*, seedlings; *f*, cotton around seedlings.

2. *With roots in damp chambers.*

Because of the slow diffusion of gases in water, other results were anticipated on growing seedlings in damp chambers. To this end an apparatus (*fig. 3*) was constructed consisting of two eight-liter bottles (*A* and *B*) which were connected near their bases by a rectangular chamber (*C*) whose inner dimensions were 1.5^{cm} by 3^{cm} by 1^{cm}. This chamber was covered entirely with plaster of Paris, except along the sides, where the plaster was removed to expose the inner side walls of glass (*a*). A large cork (*b*) was sealed into each end of the chamber, through which openings were made of the same cross-section as the chamber. The distal end of each cork was fitted tightly into the opening of the bottles (*A* and *B*). On the upper side of the plaster case was hollowed out a groove (*d*), and perforations were made through the floor of this groove in such a way that the roots of the seedlings (*e*) projecting through these holes would be suspended in a chamber of gas when *A* and *B* were filled with gas. The groove made a good support for the cotyledons and for the cotton which was wrapped around them to keep them moist. The plaster was entirely covered with a thin layer of paraffin. In this way an air-tight passage was made from one bottle to another. To insure a moist condition of the gases which filled chambers *A* and *B*, several sheets of damp filter paper were placed in the bottles, and the cotton around the seedlings was moistened frequently. Besides this, the connecting chamber was soaked in water to infiltrate the plaster before inserting the seedlings.

In such a contrivance, judging from a preliminary experiment, it was thought that the gases diffused too rapidly through the chamber to be effective. However, by testing with a mixture of illuminating gas and air in one bottle and air in the other, and observing the contortions in the roots produced by the illuminating gas, it seemed evident that the gases must diffuse slowly enough to allow a considerable difference in the gases on the opposite sides of the roots.

Seedlings of *Zea Mays*, *Lupinus albus*, *Vicia sativa*, and *Pisum sativum* were now supported in the chamber, and bottle *A*, filled with 100 per cent. CO_2 or with mixtures of air and CO_2 in varying percentages, and bottle *B* filled with air. It was found that when a mixture of 20 per cent. CO_2 and 80 per cent. air on one side was opposed to air on the other, of 18 seedlings used only 1 was positive toward the air, the remaining being indefinite; while when 100 per cent. CO_2 was opposed to air, of 18 seedlings only 2 were positive and 16 indefinite. In the former case the roots grew 5 to 10^{mm} during the experiment, while in the latter case only 0.5 to 1.5^{mm}.

Although probably there was not a very great difference in the composition of the gases on the opposite sides of the roots, there was unquestionably some difference; and, notwithstanding this, it may be seen that the roots, although influenced in growth, did not make any definite curves with references to these gases, even when 100 per cent. CO_2 was used. In nature one can hardly conceive of conditions which would give a greater difference in the composition of gases on opposite sides of the roots.

3. With roots in earth.

In the lower half of a battery jar was fastened securely with sealing wax a glass plate in a vertical position so that gas could not pass the septum. Water was placed in the bottom to the depth of 2 or 3^{cm}, and pieces of broken plant crock were thrown in loosely. A glass tube was brought down to the bottom of each chamber, with its lower end curved upward under a piece of broken crock. The whole jar was now filled with moist earth. The seedlings were planted in a line directly above the upper edge of the glass partition. A different gas was led into each chamber, having passed on its way from the gasometer through liter bottles of water, that the rate of flow might be known and kept the same for each gas.

In this experiment the roots were in practically natural conditions, except for the gases used. If they were sensitive to the gases, and responded by curving toward one or the other, then aerotropism would be demonstrated.

At first, very short seedlings were used and the gases allowed to diffuse slowly through the earth; but later, longer roots were used and the gases passed in more rapidly. In every case CO_2 was passed into one side of the chamber and air into the other, the volume of each varying from 18 to 40 liters during the experiment of 24 hours' duration. Of the 165 seedlings of *Raphanus sativus*, 31 were positive toward the air, 34 negative, and 100 were neither positive nor negative, 98 of the last being straight. In the last two sets, when the 60 seedlings were planted twelve hours before the gases were led into the chambers, the majority of the roots were straight at the close of the experiment.

In a modified form of this experiment the seedlings were planted in a vertical layer of earth or sawdust 18^{cm} long by 12^{cm}

wide by 1 ^{cm} thick, inclosed in an iron wire gauze cage which was fitted in as a partition so closely between the sides of a glass jar that gases brought into the two chambers thus formed could pass over only through the earth or sawdust. This chamber was carefully covered; the seedlings were kept constantly moist; and the CO_2, or mixture of CO_2 and air, on one side, and air on the other, were forced in from a gasometer or water stream air-pump at the same rate and equally moist. By such a method there was certain to be an access to different gases on opposite sides of the roots.

Regardless of the percentages of CO_2 used, the results were not indicative of aerotropism; 14 roots bent toward the earth through which air was flowing, 14 away, and 28 grew in the vertical plane. *Pisum sativum*, *Lupinus albus*, and *Zea Mays* (popcorn) were used in this experiment.

From these two methods of experimentation it is seen that, while 221 representative seedlings were exposed to the one-sided application of a normal pressure of oxygen as opposed to some mixture of gases having a less pressure of oxygen or none at all, and while they were otherwise in almost natural conditions, still only 45 turned toward the source of oxygen, while 48 turned away, and 128 remained neutral. Certainly no one would contend that such results indicate that the roots are aerotropic, though they do show some disturbance in the direction of growth.

4. With roots in gelatin.

In the use of gelatin a medium was found that would permit of growth of the root, while preventing a rapid diffusion of gases. Solutions of 6 or 7 per cent. of gelatin in distilled water were thoroughly saturated, when cold but before solidifying, with air, hydrogen, or CO_2, either by forcing the gas through the solution, or with the solution in an air-tight chamber by exhausting and refilling the chamber with the gas which passed through the gelatin as it entered. These solutions were allowed to harden for twelve hours, standing in chambers of air, or hydrogen, or CO_2, as the case might be, in paper-lined, rectangular dishes, 20 ^{cm} by 12 ^{cm} by 4 ^{cm}, into which they had been poured when saturated, the gelatin containing the hydrogen, or CO_2, remaining in the air-tight chamber of that gas from which it had not been removed at any time during the operation.

Two of these blocks of hardened gelatin (*fig. 4*, *e* and *e*), removed from the rectangular molds and freed of all unnecessary paper, were transferred quickly to a damp chamber (*A*), lined with moist filter paper dipping into several centimeters of water (*D*) in the bottom of the jar. The gelatin blocks were placed on their narrow sides on a raised platform of glass (*C*) supported in the bottom of the jar, so that their broad sides were vertical and facing each other. Seedlings, supported in the usual manner on the bar of wood, were now quickly placed between the blocks of gelatin, the latter were pressed together and held firmly in the vertical position by means of glass plates (*a* and *a*) and wooden bars (*d* and *d*), at their backs, the latter pressing at both ends against the sides of the damp chamber.

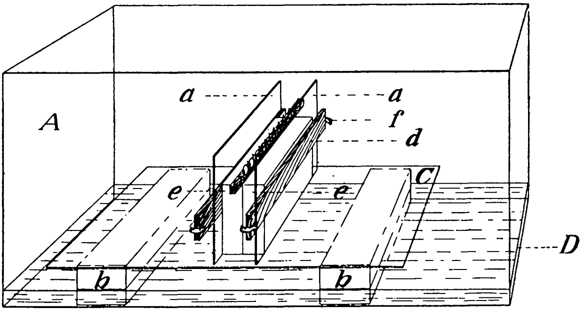

FIG. 4.—*A*, damp chamber; *D*, height of water; *C*, glass plate resting on *b*; *b*, glass jar; *e*, block of gelatin; *a*, supporting glass plate; *d*, supporting wooden bar; *f*, rubber tubing.

It may be seen from Table VI that in the first two sets of seedlings the gelatin was not thoroughly saturated with CO_2. Under such circumstances the difference in oxygen pressure on opposite sides was not great, and the seedlings had ready access to a sufficient oxygen pressure for good growth, but made no definite curves. In the other sets, in which the gelatin was thoroughly saturated with CO_2 or hydrogen, the oxygen pressure was not sufficient for good growth. Here again none of these roots showed curvatures of any definite character.

A still further trial, however, was made by supporting the roots in a very thin septum of gelatin and allowing gases to diffuse through the gelatin from the opposite sides.

TABLE VI.

(Plus sign indicates growth into gelatin containing air.)

Species	No. of ind'vs	Period: hours	Gases		+	−	o	Growth in mm.	Remarks
Lupinus albus..	15	24	CO_2	Air	5	3	7	....	Gelatin not thoroughly saturated with CO_2.
Lupinus albus..	18	30	CO_2	Air	2	11	5	....	Gelatin not thoroughly saturated with CO_2.
Lupinus albus..	16	24	CO_2	Air	6	7	3		
Lupinus albus..	13	30	CO_2	Air	5	7	1		
Lupinus albus..	7	30	CO_2	Air	..	..	7	20	
Zea Mays...... (popcorn)	11	30	CO_2	Air	2	3	6	8–28 12–27	Growth retarded during first 30 hrs.
Pisum sativum .	5	48	H	Air	1	..	8	4–20	Growth much retarded.
Lupinus albus..	4	60		Air				8–17	

A frame (*fig. 5*) was made of strips of glass cemented together along the edges and fastened at the ends in grooves in wooden bars (*a* and *e*). These strips were of two sizes. The wider ones (*b*) were so secured in the wood that narrow spaces were left between them (*c*), which were covered by the narrower strips (*d*), except in the lower 1.5^{cm}. Thus a series of little chambers was formed not more than 3^{mm} in diameter, open at the top and closed at the bottom except for the opening (*f*) between the strips of glass. By temporarily closing these openings with strips of glass the chambers could be filled with gelatin, after the hardening of which the two strips of glass could be removed. This frame with the little chambers filled with gelatin was now pressed down into a battery jar containing enough water to cover the lower bars of wood (*h*). By inserting rubber tubing between the edges of the frame and the sides of the battery jar two almost air-tight chambers were formed.

Down the middle of each column of gelatin a needle was thrust to make easy the passage of roots which were pushed down into the gelatin till the tips came below the glass covers, as shown in *fig. 5*. The chambers on the two sides of the partition were then filled with gas as desired.

In one series of experiments, in which CO_2 was passed slowly into one chamber and air more rapidly into the other, of 3 lupine, 5 pea, and 4 popcorn seedlings used, all grew nearly straight, though 2 took a somewhat slanting course toward the air chamber.

In another series, in order to reduce the surface for the cross-diffusion of the gases, the gelatin was smeared over with olive oil and the surface opposite the roots melted off with a hot needle. Thus, just as far as possible, the cross-diffusion of gases was confined to the vicinity of the root-tips, and the tips were exposed to the gases, except for the very thin covering. Air and CO_2 were introduced on opposite sides of the seedlings, and at the close of 42 hours it was found that, while there had been very little growth, there had been no curves.

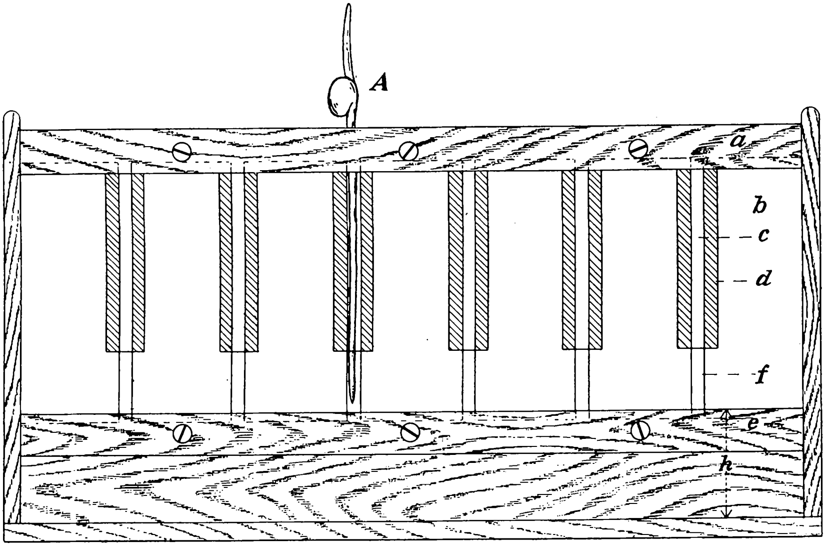

FIG. 5.—*A*, seedling; *a* and *e*, bars of wood; *b*, wide strips of glass; *c*, narrow spaces; *d*, narrow strips of glass sealed on; *h*, height of water; *f*, spaces filled with gelatin.

Thinking to determine roughly the rapidity of diffusion of gases in such contrivances as have been described above, one block of gelatin, made alkaline and colored with phenophthalein, was opposed to one saturated with CO_2, and the septum of gelatin in *fig. 5* was made pale red and the CO_2 and air brought on opposite sides as in the experiment. In the former case, within 4 hours the gelatin was decolorized to a depth of 10^{mm} and in 24 hours the entire block had lost the red color; while in the preparation shown in *fig. 5* the gelatin was entirely decolorized in 1¾ hours. Judging from these two tests, the CO_2 must have diffused rapidly enough through the gelatin to cause curves had the roots been aerotropic; and if CO_2 diffuses rapidly, hydrogen and air would diffuse even more rapidly.

Beyond doubt, in these experiments with the gelatin cultures, and especially in the last-described series, the roots have been met on opposite sides by different gases, and if they were aerotropic have been given the opportunity to show such reaction. In spite of this, under all these conditions the majority of the roots have remained straight, and the main result has been simply retardation of growth due to the diminished oxygen pressure. It is certainly difficult to conceive of any more favorable conditions under which the roots might have been placed to exhibit aerotropism.

5. *Experiments similar to those of Molisch.*

There remains only one more task, namely to determine if possible the cause of the curves which Molisch observed and termed aerotropic. To this end an apparatus was made similar to that used by him and described in the first part of this paper. It consisted of a rectangular jar containing folds of moist filter paper, having an opening on one side through which moist gases were led from a gasometer; and having a plate of cork infiltrated with paraffin sealed into the open end. In the plate were cut six vertical slits 2^{cm} long by 1 to 2^{mm} in width, and fastened to the upper edge of the closure was a ledge of cork in which was cut a longitudinal slit 5^{mm} wide. Small corks, through which projected the roots held firmly in their support with moist cotton, rested upon this ledge so that the roots passing through the slit in the ledge hung directly before, and within 2 to 4^{mm} of the slits in the cork plate closing the gas chamber.

An apparatus prepared in this way was placed in a large covered aquarium lined with and also containing many folds of moist filter paper supported on wooden bars, so as to add to the evaporating surface. The aquarium was covered with opaque black paper and the whole wrapped in black cloth. The gas, led in through an opening in the cover of the aquarium from the gasometer, was passed through a wash bottle containing water to insure a moist condition of the gas as well as to aid in determining the rate of flow.

In these experiments, pea, radish, and popcorn seedlings were used, and in the gas chamber were CO_2, hydrogen, or air. When CO_2 was diffusing from the gas chamber during 6 to 12 hours, and 17 seedlings were used, it was found that 4 were curved away from the source of CO_2, 5 toward it, and 8 were neutral; 4 of those which turned toward the gas chamber grew into the chamber through the slits.

When hydrogen was diffusing from the chamber, 7 of the 12 seedlings used curved toward the source of that gas. At the close of 12 hours it was found that there had been good growth, and that 4 roots had grown through the slits into the hydrogen chamber.

When air was diffusing through the slits in the cork plate, 10 of the 18 seedlings turned toward the air chamber, 1 away, and 7 were neutral.

The gas chamber was thoroughly aerated after each series of experiments, so that no remnant of the gas previously used could influence the results.

The most interesting results were obtained, however, when no special gas was used, but only air at rest both inside and outside the small chamber. It was found that under these conditions also curvatures were made, 4 of the six seedlings turning toward the small chamber containing air.

Altogether in this series of experiments, in which 53 seedlings were used, regardless of the gases diffusing from the chamber, 26 turned toward the gas chamber and 11 away, while 16 remained neutral. Even more striking was the observation that curves appeared in the roots whether or not a gas was passed through the slits. It must be very evident from these observations that such curvatures are not aerotropic, but are to be accounted for in some other way. It seemed not unreasonable to conclude that they were hydrotropic curves, and that, as the large chamber was probably not thoroughly saturated with moisture, the roots were turning toward the moisture emanating from the surface of the cork plate.

To verify this conclusion, a preparation was made in which the roots were placed between two cork plates set in the same damp-chamber, with the same evaporating surface as before.

Six pea seedlings were set up in the ordinary manner, the roots being 2 to 3^{mm} from each cork plate. After 2 hours, 1 root was touching one plate of cork; after 3 hours, 4 were touching this plate; and at the end of 24 hours, 2 roots were touching one cork, 2 the other, 1 was straight, and 1 had grown out beyond the two plates.

The evidence was absolutely convincing that here were purely hydrotropic curves. The cork surfaces had acted as evaporating surfaces in a chamber of the kind ordinarily said to be saturated with moisture. Accordingly it is highly probable that Molisch's damp-chamber, which had relatively less evaporating surface than mine, was not saturated with moisture and that the curves he obtained were hydrotropic rather than aerotropic.

III. DEDUCTIONS FROM EXPERIMENTS.

In my experiments, roots of *Zea Mays*, *Pisum sativum*, *Raphanus sativus*, *Cucurbita Pepo*, and *Lupinus albus* have been subjected to the one-sided access of oxygen, hydrogen, and carbon dioxid, to determine whether these roots do really curve toward or away from these gases in natural or artificial conditions.

Incidentally I have offered my solution for the curvatures of roots recorded by Molisch and by him termed aerotropic.

1. When the roots of the various seedlings mentioned in this paper were grown in water between submerged chambers, the one containing air and the other CO_2 or H, no constant and regular curvatures were observed. Under these conditions the majority of the roots were indifferent to the influence of any of these gases. The same results followed when the roots were not submerged in water, but placed between the gas chambers in a larger damp-chamber.

2. When the seedlings were grown in a thin, vertical layer of earth, forming a septum between air and CO_2, or air and hydrogen, or in earth permeated on one side with air and on the other with CO_2 or hydrogen, very few curves were formed, the large

majority of roots growing straight or, if curved, the curves were not directed by the presence of the gases.

3. When the roots of seedlings were grown in a thin layer of gelatin, between different gases, as air and CO_2 or air and hydrogen, or when grown between and enclosed by blocks of gelatin, one saturated with air and the other with CO_2 or hydrogen, no curves of constant direction were shown.

4. The preparation of experiments similar to those of Molisch, where roots were supported close to narrow slits, opening into gas chambers from which gases were constantly diffusing, brought to light the important truth that curves were produced, generally toward the gas chambers, no matter whether gases (oxygen, hydrogen, or CO_2) were diffusing from the chambers, or no gases whatever were diffusing and a like pressure of air surrounded the roots on all sides. The observations led to the discovery that these curves were purely hydrotropic.

5. Finally, from a careful consideration of the results of experiments set forth in this paper, with the large number of individuals of representative species, and the variety of methods of experimentation employed, both under nearly natural and under artificial conditions, one is driven to the conclusion that, at least so far as the representative land plants here used are concerned, definite direction curvatures are not induced in roots by the one-sided access of such gases as oxygen, hydrogen, or carbon dioxid, and their roots are therefore not aerotropic.

Thus far the evidence is decidedly against a belief in the aerotropism of roots.

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